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Relevance of the Force-Velocity Relationship in the Activation of Mono- and Bi-Articular Muscles in Slow Arm Movements in Humans

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We have investigated whether differences in EMG activity in mono- and bi-articular muscles for concentric and eccentric contractions (van Bolhuis, Gielen, & van Ingen Schenau, 1998) have to be attributed to a specific muscle coordination strategy or whether they are merely a demonstration of adaptations necessary to adjust for muscle contractile properties. Slow, multi-joint arm movements were studied in a horizontal plane with an external force applied at the wrist. Kinematics and electromyography data from 10 subjects were combined with data from a 3-D model of the arm and a Hill-type muscle model. Data for both mono- and bi-articular muscles revealed a higher activation in concentric than in eccentric contractions. The model calculations indicated that the measured difference in activation (20%) was much larger than expected based on the force-velocity relationship (predicting changes of ~5%). Although these findings eliminate the force-velocity relationship as the main explanation for changes in EMG, it cannot be ruled out that other muscle contractile properties, such as history dependence of muscle force, determine muscle activation levels in the task that was studied.

Introduction

The coordination of muscle activation by the central nervous system to produce smooth and efficient movements is far from understood. For example, the shoulder and elbow joints together have 5 degrees of freedom, but they are controlled by at least 23 muscles. It is not known how a selection is made for the particular activation of muscles for a particular motor task.

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In order to understand the dynamics of arm movements, two components can be distinguished. First, movements of the arm, such as for example during reaching, consist of linear and angular accelerations of the arm segments, which require specific forces and joint torques. Second, when a force has to be exerted on the environment, as for example in lifting a box, additional forces and joint torques are required. These additional forces are not related to the movement itself, and it often happens that the requirements for the external force (weight of the box) are different from the requirements for the movement (linear and angular accelerations) of the segments (van Ingen Schenau, Pratt, & Macpherson, 1994). This is the case, for example, when a box is placed on a shelf: elbow flexors are active to hold the box, but the elbow itself is extending. Obviously, when muscles are activated, the central nervous system has to take into account both components. However, studies of muscle coordination aimed at developing a theory on how muscle activation levels are chosen, have mainly studied movements in which the first component, the production of torques related to movement, dominated. Although the importance of gravity and other external forces has been acknowledged (Feldman, Ostry, & Flanagan, 1990; Flanders, Pellegrini, & Geisler, 1996; Soechting & Flanders, 1992), theories on muscle coordination have been developed that apply mostly to movements in free space. They cannot be applied to movements in which force has to be exerted on the environment (see Desmurget, Pelisson, Rossetti, & Prablanc, 1998, for more references; Feldman et al., 1990; Kuo, 1994; Schmidt, 1985; Soechting & Flanders, 1992; Sporns & Edelman, 1993).

A theory about muscle coordination specifically dealing with movement tasks in which force had to be exerted was proposed by van Ingen Schenau (van Ingen Schenau, 1989; van Ingen Schenau, Boots, de Groot, Snackers, & Woensel, 1992). He argued that, due to the difference in mechanical action of mono- and bi-articular muscles, the former might be used as work generators (active when shortening), while the latter might be used to manipulate joint torques such that the resulting force direction meets the specific task demands. This theory implied a clear distinction in the control of mono- and bi-articular muscles. Mono-articular muscles would be activated only while shortening (which is related to movement direction) proportional to the amount of external work that has to be done. Activation of a bi-articular muscle would be chosen such that it would redistribute the work (torque multiplied by joint angular displacement) generated by the mono-articular muscles to achieve the desired force direction of the end effector, regardless of whether the bi-articular muscle is shortening or lengthening. This division of muscles in two functional groups reduces the number of degrees of freedom for muscle activation and could thus provide a partial answer to the question how the activation of muscles is chosen.

Although the ideas described above were supported by results from various studies (Jacobs & van Ingen Schenau, 1992; Pratt, Chanaud, & Loeb, 1991; van Ingen Schenau et al., 1995; van Ingen Schenau et al., 1994), leg extension experiments by Doorenbosch and others (Doorenbosch & van Ingen Schenau, 1995; Doorenbosch, Welter, & van Ingen Schenau, 1997) that were specifically aimed at testing this theory showed that mono-articular muscle activity varied not only with force direction but also with movement direction. Bi-articular muscle activity varied with the exerted force direction as expected. However, the results were not conclusive because the leg extension experiments were performed within a small range of force and movement directions. Therefore, van Bolhuis et al. (1998) turned

towards arm experiments in which force and movement direction could be varied independently over a wider range. They found (a) that the activity of bi-articular muscles varied only with the exerted force direction and not with movement direction and (b) that the activity of mono-articular muscles varied not only with movement direction but also with exerted force direction. The original theory was slightly reformulated: mono-articular muscle activity would be chosen such that it would combine with the bi-articular muscles activity to produce the desired force direction. Consequently, the results corroborated the postulated difference in the coordination of mono- and bi-articular muscles. However, two important questions could not be answered and will be addressed in the present paper.

The first question deals with the effect of the force-velocity relationship on the activation of muscles. Depending on movement direction, muscles perform either concentric or eccentric contractions. The increased mono-articular muscle activity for movements in a particular direction (the so-called preferred movement direction, PMD) (van Bolhuis et al., 1998) could have been caused exclusively by the fact that the mono-articular muscles were shortening. When the mono-articular elbow flexor muscle was shortening during elbow flexion, the central nervous system might have increased its activity to generate the same force level as when it was lengthening during elbow extension. Van Bolhuis et al. (1998) claimed that force-velocity effects could not have been a determining factor for muscle activation because movements were performed at a very low velocity resulting in small contraction velocities. Instead, they argued that movement direction is a parameter used by the nervous system for the control of mono-articular muscle activity. However, the muscle contraction velocity was not measured, and the claim could not be substantiated quantitatively.

The second question is whether the suggestion by van Bolhuis et al. (1998), that the PMD of mono-articular muscles corresponds to the direction of maximum muscle shortening, is correct. This suggestion was based on the data of only one single muscle (brachioradialis) and with the use of a simple two-dimensional model of the arm. A definite conclusion can only be reached when muscle activation levels and preferred movement directions are compared to measured shortening velocities for various movement directions and for various muscles.

The purpose of this study was to provide quantitative data on muscle contraction velocities in order to answer these two questions. To this end, the experimental set-up from van Bolhuis et al. (1998) was replicated and the actual changes in muscle length were calculated using a state-of-the-art three-dimensional model of the shoulder and elbow (van der Helm, 1994; Veeger, Yu, An, & Rozendal, 1997).

Methods

Ten healthy male subjects (age 24 to 32 years) with no known neurological disorders participated in this study after giving informed consent. The experimental set-up was replicated as accurately as possible from that used by van Bolhuis et al. (1998). Subjects were seated at a table with the arm abducted (upper arm in line with the shoulders) and the elbow 90° flexed in the horizontal plane. The forearm was in a position approximately halfway between full supination and full pronation. This position of the arm of the subject, in which all measurements were made, will be referred to as the reference position. To avoid fatigue, the forearm was

suspended from the ceiling. The shoulder was prevented from moving back and forth by a brace mounted on the back of the chair. A horizontal force of 25 N could be applied on the wrist in three directions, using a rope attached to a bracelet on the subjects' wrist. A force (movement) direction of 0° corresponded to pulling (moving) the wrist in the direction of the elbow in the reference position. For example, a movement direction of 90° corresponded to moving the hand in the direction of elbow extension (see Figure 1). A force (pulling) direction of 90° corresponds to force exerted by the subject; in other words, the weight is pulling in the 270° direction.

Slow wrist displacements were made at a velocity of 1.5 cm/s centered at the reference position in 16 different movement directions (0, 22.5, 45, 67.5 . . . 337.5°). Force direction could be varied independently from the movement direction (see Experimental Set-Up [below] and Figure 1). The force directions tested (the pulling directions) were 30°, 90°, and 270°. These force directions were selected because (a) they require large muscle activity for the shoulder end elbow muscles, and

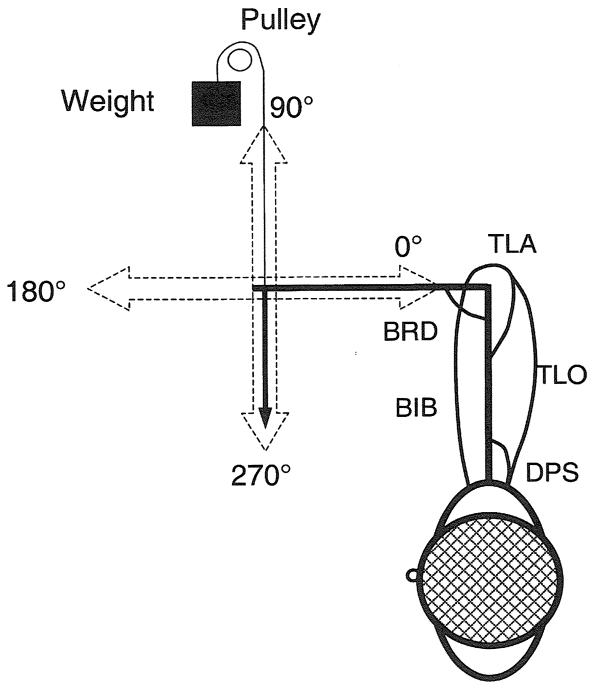

Figure 1 — Schematic drawing (top view) of the experimental set-up and muscles. The subject is sitting at a table with the elbow 90° flexed in the horizontal plane. The forearm is suspended from the ceiling. Force is applied to the wrist via a bracelet to which a rope is attached such that no forced pronation or supination is present. Force direction is changed by changing the position of the pulley. In this drawing, the subject is exerting force (black arrow) in the direction 270° (pulling direction). Movement direction 0° is when the wrist moves towards the elbow. Muscles shown are: BRD (brachioradialis), BIB (biceps caput breve), DPS (deltoideus pars spinalis), TLA (triceps lateralis), and TLO (triceps caput longum).

(b) they are representative for the force directions that show a clear distinction between mono- and bi-articular muscles (van Bolhuis et al., 1998). Electromyographic activity (EMG) was measured from three mono-articular and two bi-articular muscles acting around the shoulder and elbow joints (Figure 1). The rectified EMG (REMG) was averaged over 2 s, during which the arm passed through the reference position. It was then scaled to the maximum REMG for that muscle measured in the experiment and plotted in polar coordinates as a function of movement direction. Muscle contraction velocities were calculated with a three-dimensional shoulder-arm model using the 3D coordinates of bony landmarks from trunk and arm (see later) measured during the movement. An estimate of the effect of the force-velocity relationship was obtained using these contraction velocities in combination with a muscle model, with relevant muscle architecture parameters that were obtained from the literature.

Experimental Set-Up

The force was generated by suspending a mass of 2.5 kg from a rope running over two pulleys. Force direction could be varied by changing the position of the pulleys relative to the wrist. In this set-up, force was not perfectly constant throughout the movement due to friction in the pulleys (causing force changes smaller than 1 N depending on movement direction) and small variations in movement speed (causing force changes of ±0.5 N). The mass of 2.5 kg that was used was somewhat smaller than the 3 kg used by van Bolhuis et al. (1998), because these authors reported that some subjects had difficulty holding it. The movement range and the direction and velocity of movement were indicated to the subject by a cable with markers that rotated about two pins separated by 15 cm. A small antenna pointing downward from the wrist allowed subjects to match the wrist movement to the target. This method of movement feedback differed slightly from the method used by van Bolhuis et al. (1998), who used a second rope attached to the wrist to provide position feedback via an oscilloscope.

Protocol

Movements were made along a straight line with a velocity of 1.5 cm/s from approximately 7 cm before to 7 cm past the reference position. Subjects were instructed to make the pointer follow the target with a smooth movement without unnecessary co-contraction. The 16 movement directions and three force directions were tested in random order. For every force direction, 8 movement trials and 2 static trials were performed resulting in 30 trials (3 force directions × [8 movement + 2 static trials]) for each subject in the entire experiment, which lasted 1 hour. Each movement trial consisted of two times a back and forth movement (30–35 s per trial) so that, for two measurements in each of the 16 movement directions, eight movement trials were necessary. Between trials, subjects relieved themselves of the load to avoid fatigue by extending their arm to place the weight on the ground. This procedure differed from van Bolhuis et al. (1998), where each trial consisted of one measurement in one movement direction. Before and after the movement trials, a static trial was performed for each force direction, in which EMG was measured while the subject opposed the force in the reference position without moving his wrist. In order to obtain a measure for the background activity of muscles, EMG at rest was measured in the reference position in an unloaded

condition (i.e., without the 25 N force at the wrist).

EMG

Surface EMG was measured for five muscles (Figure 1): m.brachioradialis (BRD, a mono-articular elbow flexor), m.biceps caput breve (BIB, a bi-articular elbow flexor and shoulder ante flexor), m.deltoideus pars spinalis (DPS, a mono-articular shoulder retro flexor), m.triceps lateralis (TLA, a mono-articular elbow extensor), and m.triceps caput longum (TLO, a bi-articular elbow extensor and shoulder retro-flexor). Electrodes (Ag/AgCl electrodes, Medi-Trace, Pellet 1801, inter-electrode distance 2.5 cm, diameter 1 cm) were placed on the muscle belly parallel to the direction of the muscle fibers. The EMG signal was band-pass filtered (10–216 Hz), sampled at 800 Hz, rectified, low-pass filtered at 20 Hz, and then stored at 100 Hz (Porti-17, Twente Medical Systems, Enschede, The Netherlands).

Muscle Length

Muscle length for each muscle was calculated with the Dutch Shoulder-Elbow model (van der Helm, 1994; Veeger et al., 1997). The model contains seven bony parts (thorax, clavicula, scapula, humerus, ulna, radius, and hand) connected by ball or hinge joints. The scapulo-thoracic contact is taken into account as a pseudo joint. The 22 muscles modeled are subdivided into 110 muscle elements to represent their full mechanical effect. Bone morphology and muscle attachment sites have been determined from extensive cadaver studies (van der Helm, 1994; Veeger, van der Helm, van der Woude, Pronk, & Rozendal, 1991; Veeger et al., 1997). Muscle elements run in straight lines between attachment sites unless a bony surface prevents this, in which case the line of action is determined as the shortest line from origin to insertion over the bony surface. Nine such surfaces are present, modeled by idealized shapes. The following shapes are relevant for the present simulations: the combined tuberculum majus and minus modeled as a sphere (for DPS), the radius modeled as a cylinder (for BIB), and the elbow (olecranon) modeled as a cylinder (for TLA and TLO). Muscle length and contraction velocity were calculated with the following procedure. In each trial, the co-ordinates of bony landmarks from sternum, spinal column, clavicula, scapula, humerus, radius, and ulna were stored at 50 Hz with an OPTOTRAK (Northern Digital) motion analysis system. Because the scapula position is difficult to measure during movement, and because the shoulder was fixated, the scapula position was assumed to be constant relative to the trunk during the trials. The landmark coordinates were used to calculate glenohumeral, elbow, and pronation angles for each trial. These were then used as input for the shoulder-elbow model. Muscle length was defined as the average length of the muscle elements of each muscle. The muscle contraction velocity was calculated using the muscle length values 1 s before and 1 s after passing through the reference position.

Muscle Model

In order to make a quantitative estimate of the effect of contraction velocity on muscle force in the region of small positive and negative velocities, a Hill-type muscle model was used that has been described in detail elsewhere (van Soest & Bobbert, 1993). Briefly, the concentric force-velocity characteristic is based on

the classic description by Hill (1938). The shape of this curve is determined by the dimensionless parameter a_{rel} and the parameter b_{rel} (s^{-1}), being a/F_{max} and $b/L_{ce,opt}$ ($L_{ce,opt}$: optimum muscle length), respectively, where the parameters a (N) and b (m/s) are the usual parameters in the Hill equation. Values for a_{rel} and b_{rel} were taken from human triceps surae (van Zandwijk, Bobbert, Baan, & Huijng, 1996, mean of four subjects). The eccentric characteristic is described by a hyperbolic function, with the most relevant parameter for the present study being the "slope factor," which is set to 2.0 (Katz, 1939). This means that the slope of the eccentric part of the curve near zero velocity is twice the slope of the concentric curve near zero velocity.

For each muscle, the contraction velocities that were used to calculate changes in relative force capacity, were derived from the values supplied by the shoulder-elbow model. Velocities were expressed in fiber length per second by dividing the muscle contraction velocity (m/s) by the optimum fiber length (m). The values were then used to derive muscle force at a specific contraction velocity (Figure 2). Fiber length (FL) data (except for TLA, see below) were corrected to the optimum sarcomere length of 2.7 μm (Walker & Schrodt, 1974). For BRD, the fiber length was given by Lieber et al. (1992). For TLA, data from An et al. (1981) were used although sarcomere lengths were not reported and fiber length could not be corrected . To our knowledge, data on fiber length for TLO, DPS, and BIB are not available in the literature and values were provided by Spoor (C.W. Spoor, personal communication). Values of fiber length (FL) at optimum sarcomere length for the five muscles tested in this study are given in Table 2.

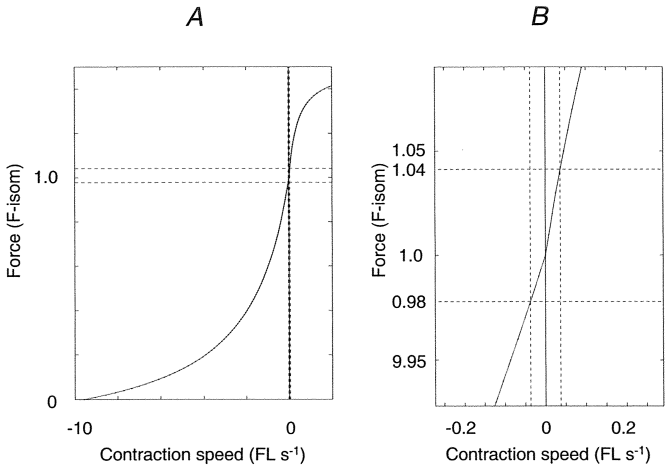

Figure 2 — Force-velocity relationship of the model. The curve shown in Figure 2A is produced from the model according to van Soest et al. (1993). Shape parameters for the concentric part of the curve (negative velocity values in fiber length per second on the horizontal axis) were taken from human triceps surae (van Zandwijk et al., 1996). The curve was calculated with activation level 1.0 (full activation) so that maximum isometric force is 1.0. Figure 2B is a magnification of the zero velocity region in Figure 2A. Vertical dashed lines indicate the maximum shortening and lengthening contraction speeds of brachioradialis during the experiment. Horizontal dashed lines indicate the maximum attainable force. See text for further details.

Table 1 Significance Values and Locations of Means of Fitted Ellipses and Directions of Muscle Shortening for All Muscles Per Force Direction Averaged Over Subjects

Muscle	FD (°)	PMD	Dist (%)	*p* value	*n*	MSD	V test	REMG diff
		mean (*SD*)				mean (*SD*)		
BRD	30			nc	9		—	ns
	90			nc	10	310 (5)	—	ns
	270	318 (43)	9.9	.003	10		.05	.001
BIB	30	48 (35)	1.3	.003	9		ns	ns
	90			nc	10	304 (11)	—	ns
	270	310 (42)	7.3	.003	10		.05	.001
DPS	30	26 (14)	11.0	.001	9		.05	.001
	90	42 (32)	4.9	.001	10	14 (4)	.05	.005
	270			nc	10		—	ns
TLA	30			ns	9		—	ns
	90	118 (24)	14.8	.001	10	129 (5)	.05	.001
	270			nc	10		—	ns
TLO	30	60 (24)	7.7	.001	9		.05	.005
	90	93 (18)	6.8	.001	10	81 (3)	.05	.001
	270			nc	10		—	ns

Note. FD = force direction; PMD = preferred movement direction; Dist = the length of the PMD vector as percentage of maximum REMG; *p* value = indicating the significance of the PMD according to the Rayleigh test; ns = not significant; nc = not calculated because REMG did not differ from the unloaded condition; *n* = number of vectors used for the PMD calculation (9 instead of 10 in a few calculations because, for one subject, trials in 30° could not be used due to technical problems); MSD = movement direction of maximum muscle shortening; V test = *p* value indicating the significant correspondence between PMD and maximum muscle shortening direction according to the v test; REMG diff = *p* value indicating a significantly higher REMG level in concentric contractions than in eccentric contractions.

Table 2 Muscle Fiber Lengths, Contraction Velocities, and Activation Levels for Selected Force and Movement Directions

Muscle	CMD (°)	FD (°)	ML (m)	FL (m)	Velocity (FL/s)	Con mean (*SD*)	Ecmean (*SD*)	Diff (%)	*p* value	Model (%)
BRD	315	270	0.28	0.148[a]	0.0374	0.70 (0.13)	0.52 (0.17)	–24.7	<.01	6.49
BIB	315	270	0.35	0.116[b]	0.0427	0.77 (0.15)	0.67 (0.14)	–12.4	ns	7.36
DPS	22.5	30	0.1	0.076[b]	0.0102	0.83 (0.16)	0.62 (0.13)	–24.7	<.01	1.82
DPS	22.5	90	0.1	0.076[b]	0.0102	0.53 (0.14)	0.42 (0.14)	–21.7	<.05	1.82
TLA	135	90	0.22	0.084[c]	0.0232	0.83 (0.10)	0.60 (0.14)	–28.7	<.001	4.08
TLO	90	30	0.39	0.091[b]	0.0169	0.64 (0.18)	0.60 (0.10)	–7.8	ns	2.99
TLO	90	90	0.39	0.091[b]	0.0169	0.75 (0.11)	0.63 (0.11)	–16.1	<.001	2.99

Note. CMD = concentric movement direction; FD = exerted force direction; ML = length of the muscle tendon complex at the time of measurement; FL = fiber length corrected to a sacromere optimum length of 2.7 μm; Velocity = absolute contraction velocity, in fiber lengths per second, that was used to calculate the force level differences (according to the muscle model) between positive (eccentric) and negative (concentric) contractions; Con, Ecc = values for concentric and eccentric muscle activity (REMG) levels. Values were scaled to the maximum absolute value obtained in the experiment (1.0); Diff = difference between concentric and eccentric REMG expressed as a percentage of concentric REMG; *p* value = significantce of the difference between concentric and eccentric REMG (one-sided *t* test); ns = not significant; Model = difference in force level predicted by the muscle model, expressed as a percentage of concentric force level.

[a]Data from Lieber et al. (1992). FL in this table is larger than given by Lieber et al. because they corrected to a sarcomere length of 2.2 μm.

[b]Data from C.W. Spoor (personal communication).

[c]Data from An et al. (1981). *Not* normalized to 2.7 μm fiber length.

Data Analysis

REMG was obtained by averaging the signal over a period of 2 s, when the wrist passed through the reference position. REMG was then scaled to the maximum activation level that was measured for that muscle and for that subject during the entire experiment. The average REMG value for a movement direction was obtained by averaging the mean activity of two measurements over the 10 subjects. Muscle activity was plotted in polar coordinates as a function of movement direction.

In order to test the dependence of muscle activity on movement direction, ellipses were fitted to EMG data in polar coordinates for the 16 movement directions for each force direction for each subject (van Bolhuis et al., 1998). This resulted in 150 (10 subjects $\times$ 5 muscles $\times$ 3 force directions) ellipses. The center positions of these ellipses were used to investigate whether muscles revealed increased activity in a particular movement direction. For mono-articular muscles, this direction has been named the preferred movement direction (PMD; van Bolhuis et al., 1998). PMD of a muscle was defined as the direction of the vector that pointed to the mean position of the ellipse center for that muscle for a given force direction, averaged over all subjects. Statistical significance for the PMD was tested using a Rayleigh test (which uses the length of the mean vector, combined with the number of vectors to determine the test statistic) (Batschelet, 1981). The correspondence of the PMD with the direction of maximum muscle shortening velocity (see below) was tested with theV-test, which is similar to the Rayleigh test but which is used to test whether a set of data points is oriented towards a predefined direction (Batschelet, 1981). A Student's t test was used to test whether REMG amplitude in a movement direction differed significantly from the rest REMG level in the unloaded trials. In order to test whether muscle activation level was different between concentric and eccentric contractions, a Student's t test was used. For all statistical tests, a significance level α of .05 was used.

Muscle shortening velocities were plotted in polar coordinates as a function of movement direction in the same way as the REMG activity data. The direction of maximum muscle shortening was calculated with the following procedure. First, the movement directions in which muscle shortening occurred were averaged. Second, the movement directions in which muscle lengthening occurred were averaged. Since the average direction of the lengthening values is exactly opposite to the average of the shortening values, 180° was added (or subtracted) to the direction of the lengthening average, after which the mean of these two values was taken as the direction of maximum muscle shortening.

The values for the contraction velocities (Velocity column of Table 2) that were used in the model calculations were the mean absolute values (10 subjects) of the highest concentric and eccentric contraction velocities. For example in BRD, the mean of the velocities for movement directions 315° (concentric) and 135° (315 – 180°; eccentric) was used, because 315° is closest to the calculated direction of maximum muscle shortening of 310° (Table 1) for this muscle.

Results

The forward to backward displacement of the shoulder marker on the acromioclavicular joint was largest during wrist movements in the directions 0° and 180°, where it was found to be only 4 mm (*SD* = 2 mm). This small change in shoulder position relative to the much larger elbow displacements (140 mm) in these

conditions was considered as support for the assumption that the scapula was sufficiently fixated, which was a necessary requirement for the calculation of the muscle lengths during the movements. Maximum angular velocity during the movements was 6°/s (SD = 2°/s) in the elbow and 2.5°/s (SD = 0.5°/s) in the shoulder joint.

As explained in the Methods section, care was taken to prevent any artifacts from fatigue during the experiment. For that reason, REMG was determined for the static situation before and after each set of movement trials for a particular external force. The data from the static measurements revealed no statistically significant difference (two-sided Student's t test) between REMG amplitude before and after a set of movement trials for any force direction. This justifies the conclusion that fatigue had not occurred during the experiments.

REMG As a Function of Movement Direction

Figure 3 shows polar plots of REMG for various muscles (rows) and force directions (columns) averaged over 10 subjects. The fourth column shows polar plots of contraction velocities for each muscle. The thick continuous lines in the first three columns indicate REMG values averaged over 10 subjects, and the thin dotted lines indicate the standard deviation relative to the mean. In the polar plots, a data point in the center of the circle indicates zero activity. The outer circle in each plot for REMG corresponds to maximum activity. The thick dashed circles in the plots in the first three columns are incorporated for easy reference. They indicate the average muscle activity (10 subjects) during the static trials—in other words, with the arm in the reference position generating an isometric force in each of the three directions.

In the 30° force direction (30° column) the arm is pulled backwards by the subject (pulled forward by the weight). The most important muscles for this action are DPS and TLO (Figure 3I and Q) which both have a mechanical contribution at the shoulder in retroflexion. DPS has a tendency for larger activation in movement directions near 22.5°. Statistical analyses revealed that activation of DPS demonstrated a PMD of 26° (SD = 14°; Table 1). The PMD was only calculated when the REMG during movements differed significantly from REMG in the unloaded condition for all movement directions. Significant PMDs are indicated by a dashed line from the center to the edge of the polar plot. PMDs for the other muscles are drawn in each of the circles in the rows and columns in Figure 3 and are summarized in Table 1. The small activity of both elbow flexors BRD and BIB in force direction 90° (Figure 3B and F) during movements did not differ from the REMG in the unloaded condition. Presumably, it reflects activity related to stabilization of supination/pronation of the wrist. It was not considered as important co-contraction. The absence of activity of DPS, TLA, and TLO in force direction 270° (Figure 3K, O, S) indicates that subjects performed the task without undesired co-contraction.

In order to compare the PMDs of the muscles with the movement directions corresponding to maximum muscle shortening, the dLoi/dt column of Figure 3 shows muscle shortening velocities (cm/s) as a function of movement direction. Each polar plot in this column shows the muscle shortening curves for all three force directions superimposed. These curves should be identical because arm movements should be the same for each force direction. The thick solid lines indicate mean shortening velocity (10 subjects), and the thin dotted lines indicate standard

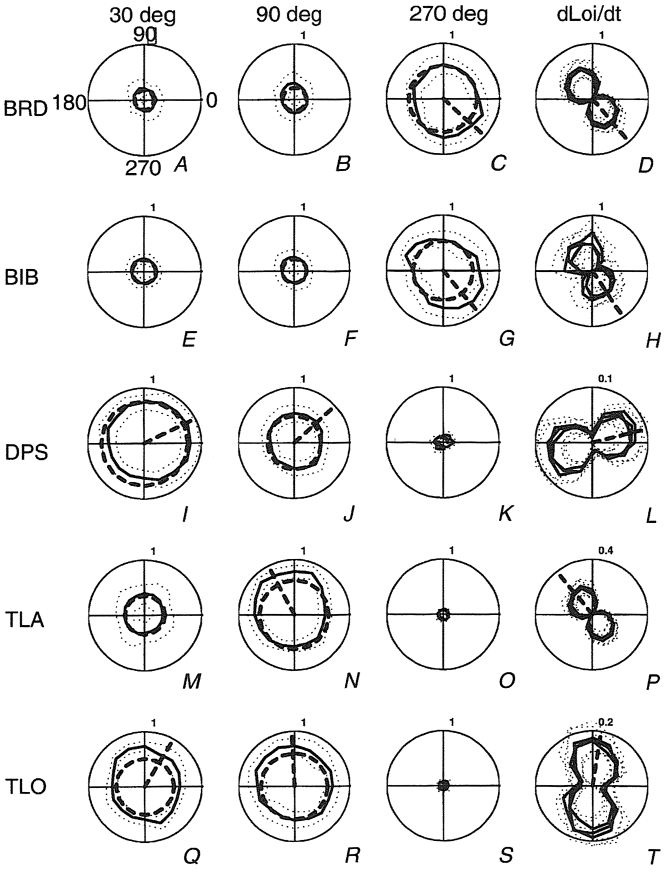

Figure 3 — Polar plots of the activity of muscles (rows) as a function of movement direction for different force directions (first three columns) of the wrist. The averaged REMG (thick line) and standard deviation (thin dotted lines) are indicated. The thick dashed circle indicates the REMG level in the static situation, where force is exerted without moving the wrist. The straight dashed line indicates the preferred movement direction (PMD). The fourth column shows polar plots of muscle shortening velocities as a function of movement direction. Thick lines are the average curves for each force direction. Thin dotted lines are standard deviations. The scale of velocity (radius of circle) is indicated on top of each plot in cm/s. The thick dashed line indicates the direction of maximum muscle shortening.

deviation relative to the mean shortening velocity. It appears that muscle-shortening curves did not change significantly for different force directions. Note that the scale for the contraction velocities is different for different muscles. Each plot in the dLoi/dt column has a figure eight shape, with two circles in opposite directions. One circle corresponds to muscle lengthening velocities, and the other refers to muscle shortening velocities. The directions that correspond to the maximum muscle shortening directions (indicated by the straight dashed line) are: 310° (BRD), 304° (BIB), 14° (DPS), 129° (TLA), and 81° (TLO) (see Table 1). In the movement directions near 45° and 225°, BRD is neither shortening nor lengthening.

In these directions, all wrist movements are generated by flexion or extension in the shoulder.

Figure 3 shows that the preferred movement directions (straight dashed lines in the first three columns) are close to the movement directions corresponding to the highest shortening velocity. A statistical analysis, using the V-test (Table 1, V test column; Batschelet, 1981), revealed that the PMD coincided with the movement direction with largest shortening velocity.

REMG Compared With Muscle Model Data

The results of the quantitative analysis of the effect of contraction velocity on muscle force are presented in Table 2 and Figure 3. Figure 3 (dLoi/dt column) shows the muscle contraction velocities in cm/s. These contraction velocities have been converted into fiber lengths per second in the Velocity column of Table 2. Table 2 also shows the model predictions of the relative difference in muscle force of the maximum muscle lengthening velocity compared to maximum shortening velocity (Model column), and the corresponding relative difference of REMG that was measured (Diff column), for a selection of force directions in which muscles were active. The data in the rows of Table 2 correspond to data in the Figures 3C, G, I, J, N, Q, and R, respectively. When a force increase is predicted (positive numbers in the Model column), a compensating decrease in REMG level (negative numbers in the Diff column) would be expected to maintain the same force level. In all cases the predicted difference in force was smaller than the difference in REMG. The largest predicted difference in force between the concentric and eccentric contractions was for BIB (BIB 315°, corresponding to Figure 3G) and was only 7.36%. The measured difference in REMG level in the eccentric (Ecc column) and concentric contraction (Con column) was 12.4% (Diff column). The ratio between measured and predicted difference in REMG was between 1.67 (for BIB) and 14 (for DPS).

The effect of the force-velocity relationship on muscle force at the contraction velocities from the present study is illustrated in Figure 2. This figure shows the force-velocity curve of the muscle model described in the Methods section. Figure 2B is a magnification of Figure 2A in the zero-velocity region. The two vertical dashed lines indicate the maximum concentric and eccentric contraction velocity measured in our study. Horizontal lines indicate the corresponding force levels relative to the maximum isometric force. The curve was calculated with active state equal to 1.0, resulting in a value of 1.0 for the maximum isometric force. This choice of active state is arbitrary because it has no effect on the relative force changes that are considered in the present study. It can be seen that despite the "steepness" of the curve in this region, the change from concentric to eccentric contraction causes only a small increase in force.

Discussion

Force-Velocity Relationship

The first aim of this study was to examine the activation of arm muscles for various movements directions and external forces. The first result of this study is that the movement direction giving the largest amount of REMG activity for a muscle corresponds to the movement direction giving the maximum muscle shortening

(Figure 3 and Table 2). The most obvious explanation for this observation is the force-velocity relationship of muscle. Yet, model calculations suggest that changes in REMG magnitude cannot be explained as an accommodation to changes in muscle force due to the force-velocity relationship (Table 2). This issue will be discussed in the next paragraphs.

A first glance on the data might suggest that the force-velocity relationship of muscles explains the REMG changes as a function of movement direction. From Figure 3 and Table 1, it is obvious that muscles tend to have a larger activation when they are shortening, and a smaller activation when they are lengthening. When the force that has to be generated remains the same, this behavior can be expected based on the force-velocity relationship of muscles. Further support comes from the comparison of activation levels during movement and static trials. Especially the mono-articular muscles DPS, TLA, and BRD show larger (smaller) amounts of activity during shortening (lengthening) than in the static condition (compare REMG in Figures 3C, I, J, and N for movement directions of maximum muscle shortening and lengthening shown in dLoi/dt column). Moreover, the concentric REMG levels were significantly higher than the eccentric REMG levels for each muscle. In a previous study, a similar change in REMG of m.biceps brachii, after switching from concentric to eccentric contractions at loads and velocities comparable to those in the present study, was also attributed to the force-velocity relationship (Heckathorne & Childress, 1981).

Van Bolhuis et al. (1998) argued that the difference in force due to force-velocity effects could not explain the larger activation during shortening of the mono-articular muscles, since the movement velocity of the wrist would be too low, resulting in rather low muscle contraction velocities. In fact, the slow movement velocity was chosen by van Bolhuis et al. (1998) in order to avoid effects related to the force-velocity relationship. The model calculations in the present study have shown that this assumption was justified, because force changes of only about 5% have to be expected with the low contraction velocities used in this study. Assuming a linear relationship between REMG amplitude and force (as in isometric contractions; Hof, 1984) in the present range of movement velocities, the small change in REMG that should have occurred due to force-velocity effects could not explain the relatively large changes in REMG (up to 20%) found by van Bolhuis et al. (1998) and in this study. The changes in REMG that were found could only be explained by the force-velocity relationship if the contraction velocities had been at least 4 (BRD) to 16 (DPS, force direction 30°) times faster than those that were actually used.

In addition to this, it must be noted that the difference in force output predicted by the model is a high estimate for two reasons. The first reason is that the model parameters that were used were taken from a relatively "slow" group of human triceps surae muscles. This results in a relatively steep force-velocity curve near zero velocity. Often, data from faster (animal) muscles are used in model calculations. This would reduce the predicted force difference by as much as a factor of 2, resulting in an even larger discrepancy between predicted and measured differences. The second reason that a 5% force difference is a high estimate is that fiber pennation angle was not incorporated in the contraction velocity calculation. Consequently, muscle length changes were assumed to be caused by fiber (sarcomere) shortening only instead of by a combination of shortening and changes in orientation of muscle fibers. In conclusion, it seems that the force-velocity

relationship cannot provide a quantitative explanation for the increased REMG amplitude for shortening contractions in the arm movements.

Two alternative explanations based on contractile properties can be proposed for the finding that the predicted changes in REMG from the muscle model were more than four times smaller than the actual REMG changes. In both explanations, it is speculated that contractile properties of muscle, which are not incorporated in our muscle model, can cause an underestimation of the predicted change in force. The first explanation is that at very low contraction velocities the force-velocity curve may be steeper than in our model. At contraction velocities below 10% of the maximum contraction velocity a second, extra steep curve has been found in frog muscles (Edman, 1988, 1993). In this range even small changes in velocity result in considerable changes in maximum force. In the context of the present study, this would lead to a larger effect of the force-velocity relationship.

The second explanation is related to the history dependence of muscle force. *History dependence* refers to the decrease or increase of isometric muscle force directly following shortening or lengthening contractions, respectively. This phenomenon has been demonstrated in vitro in animal muscles (Abbott & Aubert, 1952; Herzog, Leonard, & Wu, 1998; Meijer, 1998) and in situ in human muscles (de Ruiter, de Haan, Jones, & Sargeant, 1998). For example, de Ruiter et al. (1998) have shown that the isometric force after electro-stimulation in the human adductor pollicis muscle is dependent on both the contraction velocity and the amount of angular displacement of the thumb directly preceding the isometric measurement. Up to a 37% smaller force was produced after larger shortening distances, and the decrease in force was largest when the contraction was performed at a low velocity (6°/s thumb adduction). The history-dependence phenomena agree qualitatively with the changes in REMG levels that were found in the present study. After all, the movement directions with maximum muscle shortening (or lengthening) are also the directions in which the muscles shortened (or lengthened) over the largest distance before passing through the reference position. Instead of interpreting the data as a correlation between REMG and the speed of muscle shortening, the data could also be interpreted as a correlation between REMG and the amount of muscle shortening. Moreover, the contraction velocities were very low, which was found to have an enhancing effect on force decrease after a given distance of muscle shortening (de Ruiter et al., 1998; Herzog, 1998). Therefore, the data that are presented in Figure 3 and Table 2 could be a reflection of history dependence effects in vivo.

Several additional explanations can be given for the for the discrepancy between the measured and predicted REMG activity in eccentric and concentric contractions. Depending on the movement direction, the required joint torque could have been generated by a different distribution of activity between muscles—in other words, an increase in activity in one muscle accompanied by a decrease in an other muscle. However, since we measured activity in the main muscles across a joint, and simultaneous increases and decreases within a muscle group were not found, this mechanism can be discarded. It could also be argued that TLA and TLO increased activity when shortening because the constant level of co-contraction that was found in BRD and BIB generated a increased flexor torque around the elbow when these muscles were lengthening. However, this mechanism cannot explain why BRD and BIB changed activity when shortening because no extensor co-contraction was present. Finally, the relative contribution by recruitment

and firing rate could be different in eccentric and concentric contractions, such that the same amount of force is obtained by various combinations of recruitment and firing rate, giving rise to different REMG levels. Evidence for a different recruitment pattern in different types of muscle contraction has been provided by several studies (Nardone, Romano, & Schieppati, 1989; van Bolhuis, Medendorp, & Gielen, 1997). However, the present experimental data in the literature do not warrant quantitative verification of this hypothesis.

Mono- and Bi-Articular Muscles and Direction of Maximum Muscle Shortening

The second aim of this study was to investigate whether the PMD of mono-articular muscles was related to the direction of maximum muscle shortening. The fact that these directions coincide is illustrated in Figure 3 and Table 1. However, an important difference exists between our data and those from van Bolhuis et al. (1998), because we found a clear PMD for mono-articular as well as for bi-articular muscles.

Van Bolhuis et al (1998) found that for mono–articular muscles, the graphs (such as in Figure 2) showed a distinct offset towards the PMD, often with elliptical shapes. For bi-articular muscles, this offset was not present, and the graphs showed circular shapes centered around the origin. When the first three columns in Figure 3 are compared to the data from van Bolhuis et al. (1998), two observations can be made. First, in contrast to van Bolhuis et al. (1998), we did not find that the mono- and bi-articular muscles behave differently when activation levels are plotted as a function of movement direction. For instance, the patterns for BRD and BIB are almost identical (Figure 3C and G). Second, although the PMDs of mono-articular muscles BRD, DPS, and TLA are comparable to the PMDs found by van Bolhuis et al. (1998), they found a more pronounced orientation towards the PMD for mono-articular muscles. This is quantified in the distance of the average ellipse center location to the origin which, for BRD and DPS, was smaller in the present study than in the study from van Bolhuis et al. (1998; Table 1, Dist column).

The fact that the results from the present experiment differ from those obtained by van Bolhuis et al. (1998), although their experimental set-up was replicated as closely as possible, justifies some extra remarks. Several factors could explain the difference. In a separate experiment, the possible effects of electrode placement, movement speed, load, and inter-subject variability, were tested (data not shown), but none of these factors was found to cause different activation curves for mono- or bi-articular muscles. Two differences between the experimental protocols in the present study and the study of van Bolhuis et al. (1998) remain candidates explaining the difference. First, in the present study, only one rope was attached to the wrist. In the set-up of van Bolhuis et al. (1998), one force was applied exactly as in the present study, but an additional 6 N was exerted with an extra rope that was used for the position feedback system. This may have caused a change in the total resultant force on the wrist depending on the angle between movement direction and force direction. The second difference concerns the sequence of measurement trials. In the present study, four measurements at the reference position were performed until the load was released (see Methods). In the study of van Bolhuis et al. (1998), the load was released between each measurement. This dif-

ference in protocol may be significant in the light of the history dependence of muscle force mentioned above, because force release almost instantaneously abolishes any history-dependence effects (Abbott & Aubert, 1952; de Ruiter et al., 1998).

Concluding Remarks

The shortening velocity of the muscles has only a marginal effect on muscle activation in the present task. The assumption made by van Bolhuis et al. (1998), that force-velocity relationship effects were small enough to be neglected, is supported by the muscle model calculations. However, the fact that REMG is clearly related to movement direction leads to the suggestion that history dependence of muscle force could be a factor contributing to the changes in REMG. It seems necessary to account for this phenomenon in the muscle model (Herzog, 1998; Meijer, Grootenboer, Koopman, van der Linden, & Huijing, 1998).

The movement direction with the highest muscle activity coincides with the movement direction of the highest muscle shortening velocity. The fact that this is true for both bi- and mono-articular muscles does not support suggestions of a different functional role of mono- and bi-articular muscles (van Bolhuis et al., 1998; van Ingen Schenau, 1989).

The present results argue in favor of a low level muscle activation mechanism that uses only muscle contractile properties as the main determinant of muscle activation. Before postulating the presence of any other more sophisticated muscle activation mechanism, these low level mechanisms, such as history dependence, must be investigated first.

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